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THE BUTTERFLIES OF THE ISLE OF PINES, CUBA: EIGHTY YEARS ON

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ABSTRACT

This account extends the first substantial report of the butterflies of the Isle of Pines, which included 65 species collected for Carnegie Museum of Natural History during 1910, 1912, and 1913, from our fieldwork in 1975–1976 and 1993–1995. One hundred eleven species have now been reported from the island, and distributional data are presented for all recent records. The list includes 64% of the Cuban fauna recorded from less than 2% of the total land area of Cuba; proportional representation of taxonomic families and endemic taxa in Cuba are considered. The island comprises two distinct parts: the cultivated, populous, and severely damaged northern two-thirds, including hill ranges; the low, relatively undisturbed, dry forest of the southern one-third, separated by a swamp, the Ciénaga de Lanier. Species numbers for pooled localities north of the Ciénaga are comparable with those of the south, but diversity in the north is concentrated in very small species-rich enclaves. These northern sites are faunal relicts; they are vulnerable and they are unprotected, stressing the need for conservation of the southern forest zone. Wet and dry seasonality is considered, and the need for phenological data for further assessing the fauna is discussed. Origins of the fauna are considered in the context of lack of phenotypic divergence between Isle of Pines and main-island populations, and the late Pleistocene is proposed as a major colonization period, with continuing two-way dispersive interchange across the Gulf of Batabanó viewed as probable. Genetic analysis of three species shows close correspondence between Isle of Pines and main island populations. The fauna is compared with that of Cuba, in general, and of an ecologically equivalent region of western Cuba, in particular.

KEY WORDS: Cuba, genetic analysis, Hesperioidea, Papilionoidea, phenology, Pleistocene, relict populations, zoogeography

INTRODUCTION

Topography and Climate

The Isle of Pines (Isla de la Juventud) lies off the southwestern coast of Cuba, due south of the boundary between the provinces of La Habana and Pinar del Río, and is independently administered by the central government. Separated from the main island by the shallow Gulf of Batabanó, the closest approach is ca. 51 km. Its land area is ca. 2200 km^2, or less than 2% of the area of the main island. The island is geologically and ecologically composed of two very different parts. The northern two-thirds of the island (ca. 1350 km^2) is Jurassic in age

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(Lewis and Draper, 1990), some parts formerly bearing extensive forests of pine (*Pinus occidentalis*), and includes three main groups of hills of which the highest point is just over 310 m at Pico La Cañada. This region is plentifully supplied with rivers. In contrast, the southern one-third of the island (ca. 770 km^2), the Llanura Cársica del Sur, is of low elevation, of late Pleistocene age (Webb, personal communication), and covered with dry, largely undisturbed semideciduous limestone forest. The difference between the two regions is so dramatic that several early maps suggested two islands instead of one (Jiménez, 1976). The two regions are linked by the Ciénaga de Lanier, a fresh-to-brackish swamp oriented east to west and open to the sea through mangrove at either end, irregular in outline, and without precise limits but covering an estimated 80 km^2 (Fig. 1).

A summary of climate has been provided by Gort et al. (1994) based on records from 1975 to 1987. In common with western Cuba, the Isle of Pines has a well-defined dry season from November through April, and wet season from May through October. The wettest months are June and September (each with 207 mm) and the driest December (34 mm) and March (31 mm). The mean annual temperature is 25.4°C, with maximum and minimum monthly means (July and February) of 27.9°C and 18.3°C. In April and May strong, dry southerly winds reach the island, backing to easterly or southeasterly during summer; at other times winds are predominantly easterly, inclining to northeasterly in winter.

Historical Background

The Isle of Pines had a long history of indigenous, pre-Hispanic Taino presence, but the subsequent history of colonization is both complex and unusual, being almost restricted to the northern part of the island. After 1576, when the island was placed by Crown Grant into the hands of Jerónimo de Rojas y Avellaneda, the region north of the Ciénaga de Lanier was settled for cattle raising and agriculture, although remaining thinly populated. Around 1760, almost the entire northern area was purchased by Nicolás Duarte and divided into seven circular haciendas or *hatos,* later subdivided into smaller farms (Jiménez, 1976). From the late 16th to the early 19th centuries the island was regularly visited for water and food by a succession of French, Dutch, and English pirates and freebooters.

A summary of the more recent history of the island is essential for understanding its cartography and locality records of early butterfly collections, mentioned below. The main town of Nueva Gerona was founded in 1830, Santa Fé (La Fé) soon after, and throughout the 19th century, the north of the island supported a small population, principally of subsistence farmers and fishermen of Cuban and Spanish origin. A dramatic change in the colonization pattern followed the Spanish-American War of 1898. Although Cuban independence was established by the United States Congress in 1902, Article 6 of the Platt Amendment excluded the Isle of Pines from Cuban jurisdiction, "the title of ownership thereof being left to future adjustment by treaty." Formal attachment of the Isle of Pines to Cuba was delayed until 1925. In the interim, the island was de facto open to the United States; extensive areas of the northern two-thirds of the island were purchased by North American entrepreneurs from the Spanish and Cuban owners and divided into parcels offered for citrus cultivation. While many were purchased by North Americans, only some 400 colonists actually arrived to work the land. These rectangular plots dominate maps of the period (e.g., Giltner, 1904), together with the new riverside settlements established by the immigrants. The most notable of

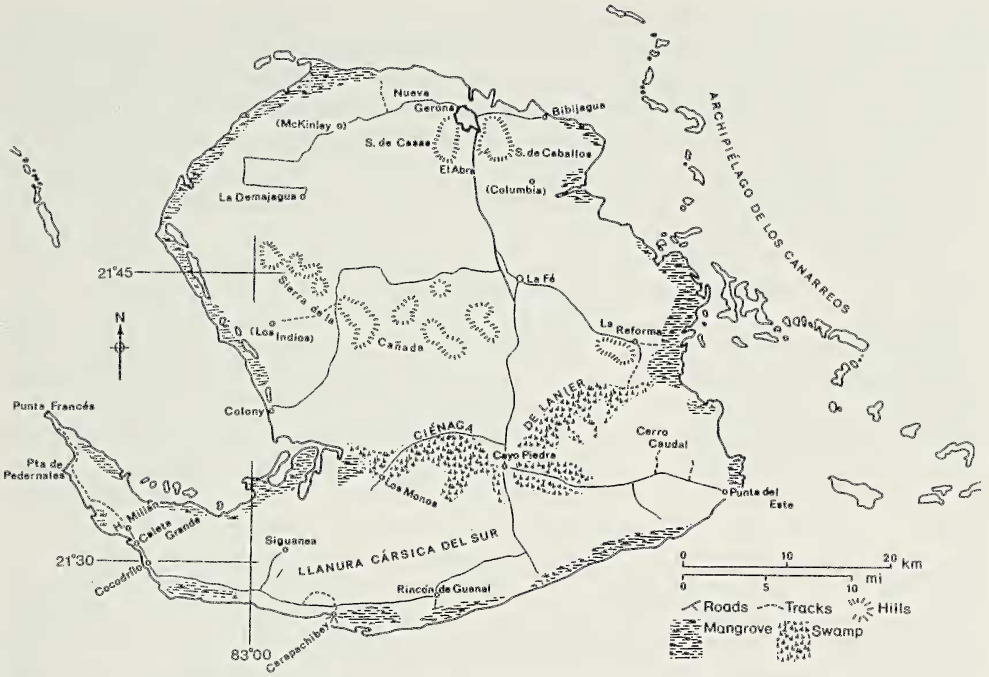

Fig. 1.—Map of the Isle of Pines showing roads and approximate location of tracks used in the 1993–1995 survey, omitting other roads, rivers, and dams (after *Municipio Especial de la Isla de La Juventud* [1983] and *Mapa Turistica* [1991]). Names of early North American townships are shown in parentheses, with their approximate positions (from Giltner, 1904).

these settlements were Columbia, McKinley, and Los Indios (Fig. 1); townships that long since have disappeared from maps of the island but which are recorded on most labels of early butterfly specimens.

The decline of these settlements was initiated by the return of many colonists to the United States following recognition of Cuban sovereignty, by the devastating hurricane of 16 August 1926, and by the onset of the Depression (Aguardo, personal communication). Columbia, the first American colony, was abandoned by 1926; McKinley and Los Indios soon followed. The former site of Columbia is now heavily cultivated for plantains, sweet potatoes, onions, and other crops. A reservoir and agricultural land cover the former site of McKinley, while Los Indios survives, at least in name, in an area that includes another reservoir, grapefruit orchards, pinelands, and a sandy, protected tract rich in endemic plants. The two reservoirs mentioned above are part of an extensive program of river damming, completed during the 1970s, that further changed the map of the island north of the Ciénaga de Lanier.

The recent history of the southern Llanura Cársica del Sur has been entirely different, its minimal colonization reflecting its inaccessibility and the harshness of its dry, forested terrain (Fig. 1). The 18th century *hatos* stopped at the Ciénaga, while early maps (e.g., Pichardo, 1860–1872) show two access tracks across the Ciénaga, in the east at "Paso de Piedras," the present site of Cayo Piedra, and at Los Monos in the west, which remain the only land links for vehicles. These maps show horse or foot trails through the forest with named but now vanished

sites including Candel, Palma Alta, El Jorobada, Acosta, and Llevat. On the southwest coast the small settlement of Jacksonville was established around 1904 by colonists from Grand Cayman Island; now named Cocodrílo, this village has a population of about 200. Isolated cottages are situated at Hato Milián, Siguanea, Rincón de Guanal, and Playa Blanca, and a meteorological radar station is established at Punta del Este. Between 1920 and 1930 the village of Carapachibey comprised 20–30 dwellings of charcoal burners; this village has vanished but a modern lighthouse was built nearby.

Entomological Studies

Field studies on the insects of the Isle of Pines have been carried out on sporadic and long-separated visits. The first records of the island's butterflies, some 13 species, were published by Poey (1854*a,* 1854*b,* 1861) from specimens collected by Juan Gundlach during a two-week stay early in 1854, when the celebrated naturalist also obtained land snails, reptiles, and birds. Over half a century later, expeditions from Carnegie Museum of Natural History provided the foundation of knowledge of the island's biotas; in some instances these remain the only source of information. The first extensive insect collections were made J. L. Graf and G. A. Link, members of an expedition in the spring of 1910, and later by Link, who returned to the island from early 1912 to June 1913. An account that included some 65 butterfly species was published by Holland (1916), and reports on other groups followed: the Orthoptera (Holland and Kahl, 1916; Bruner, 1919), Odonata (Kahl, 1916), Rhynchota [i.e., Hemiptera–Heteroptera] (Heidemann and Osborn, 1917), Hymenoptera (Rohwer and Holland, 1917), and Coleoptera (Holland and Schwarz, 1917). Locality labels on this butterfly material in Carnegie Museum show that over 90% were collected at Nueva Gerona, and the remaining few were taken in the townships of Columbia, McKinley, Los Indios, and Santa Fé. The entire southern area is represented by only a single specimen of *Eurytides celadon* collected in 1912 at Calheta Grande, on the southwest coast. No additional localities are mentioned in accounts of other insects except for some beetles from "Caballos mountain" (Holland and Schwarz, 1917), a hill east of Nueva Gerona, and it is clear that the entomological collecting at that time centered on the new American settlements.

A few specimens of historical interest obtained during the early years of the century, prior to the Carnegie expeditions (Table 1), are preserved in museum collections. Specimens collected by a W. R. Zappey are held at the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, and data labels of others in the National Museum of Natural History, Washington, D.C., document collections made at Columbia in 1903 and 1913 by H. B. Hill. Other names attached to Isle of Pines specimens that bear no date include "Zappalorti" and "Palmer and Riley."

The fieldwork carried out on the Isle of Pines between 1910 and 1913 on behalf of Carnegie Museum was a remarkable contribution to knowledge of Cuba's butterfly fauna. The collections of Graf and Link enabled Holland (1916) to list 65 species, while noting that Link, who obtained most of the museum's specimens during over a year on the island, was primarily engaged in collecting birds and ". . .gathered specimens of such insects as he encountered at times when he was not otherwise engaged." Although Graf and Link worked almost exclusively outside the southern forest, the collection of butterflies published by Holland com-

prises over half the present count for the island. Here we present the first comprehensive account of the butterfly fauna of the island since 1916, with consideration of the present distribution, conservation status, possible origins, and relationship of the insular fauna to that of the main island of Cuba.

One of the present authors (LRH), with G. Alayón and L. Zayas, carried out fieldwork on bimonthly visits during 1975 and 1976, each of three to five days and covering every month, during a general survey of the island's insects. A few of the species newly recorded at this time were mentioned by Alayo and Hernández (1987) and all are included here. As part of a collaborative research program on butterfly diversity in Cuba between the National Museum of Natural History (Habana) and the Hope Entomological Collections (Oxford University), we recently have worked on the Isle of Pines on four visits: 3–8 July 1993 (LRH, DSS, ND), 24–28 March 1994 (LRH, DSS), 25–29 August 1994 (LRH, DSS), and 17–22 March 1995 (LRH, DSS). During these visits approximately one-third of the field time was spent south of the Ciénaga de Lanier and two-thirds in northern localities.

Botanical Studies

A short account of the plants of the island was prepared by Britton (1916); an extensive work by Jennings (1917) followed, based largely on the herbarium of Carnegie Museum. Jennings provided a survey of 19th century botanical collections; he also worked on the island with Link in May 1910, and his account also credits material obtained by Link at Nueva Gerona (May–June 1912) and Los Indios (November 1912). Jennings recorded 757 plant species and cited Britton's (1916) extrapolated estimate that ". . .the total natural flora of the island is not less than one thousand five hundred species." The same figure has been given recently for the higher plant taxa of the Isle of Pines (Gort et al., 1994). A general account of the phytogeographic zones of Cuba, including the Isle of Pines, is provided by Samek (1973).

TABULATION OF RECORDS

Nature of Records

We have no ecological information on the localities in which Link and Graf collected the material published by Holland (1916), other than noting that virtually all were obtained north of the Ciénaga de Lanier. It is unlikely that any of their localities have survived, and therefore in this work all 1910–1913 records are grouped together (Table 1). In tabulating the 1975–1976 records, all localities north of the Ciénaga have been grouped together and separated from those of the southern forest (Table 1). Most of the former localities were resurveyed in 1993–1995, but the two data sets, obtained 20 years apart, are not strictly comparable. First, intensive and complete listing of butterfly species was not a primary objective of the earlier survey; and second, continuing habitat degradation over the two decades has changed or obliterated some sites. Notably, western coastal localities, the Sierra de La Cañada, and the white-sand zone of Los Indios were considerably less damaged and more species-rich in 1975–1976 than during recent visits. However, records south of the Ciénaga for 1975–1976 and 1993–1995 are directly comparable; habitats surveyed during both periods were essentially unchanged, but the area west of Cocodrílo (Fig. 1) was not visited in the earlier work. Localities north of the Ciénaga are arranged in three approximate geograph-

Table 1.—*Tabulated butterfly records (+) from the Isle of Pines including: 1910–1913 collections for Carnegie Museum in Holland (1916) with three early records (++) from other sources (see Results and Discussion); 1975–1976 records from south of the island, with the remainder of localities grouped together; 1993–1995 records tabulated in geographic zones (North, East, West, South). s: sight record. Localities are described in Tabulation of Records and shown in Figure 1. Taxonomic notes clarifying listings in Holland (1916) are given in the Results and Discussion section.*

Taxon	1910–1913	1975–1976		1993–1995			
		Other	South	North	East	West	South
Danaidae							
Danaus eresimus tethys (Forbes)							+
Danaus gilippus berenice (Cramer)	+	+	+	+	+	+	+
Danaus plexippus (Linnaeus)		+	+		+		+
Anetia briarea numidia (Hübner)		+		s			
Satyridae							
Calisto h. herophile (Hübner)	+	+	+	+	+	+	+
Calisto sibylla smintheus (Bates)		+					
Nymphalidae							
Doxocopa laure druryi (Hübner)		+	+	+	+		+
Asterocampa idyia (Geyer)		+	+				
Siderone galanthis nemesis (Ill.)	+		+	+	+	+	+
Memphis e. echemus (Doubleday)			+				
Marpesia e. eleuchea (Hübner)	+	+	+	+	+	+	+
Marpesia chiron (Fibricius)		+					
Colobura dirce (Linnaeus)		+			+		+
Historis o. odius (Fabricius)	+	+	+	+	+		+
Historis acheronta semele (Bates)					+		
Hamadryas amphicloe diasia (Fruh.)		+					
Lucinia s. sida (Hübner)	+				+		+
Eunica tatila tatilista (Kaye)			+	+	+		+
Eunica monima (Cramer)	++			+	+		+
Adelpha iphicla iphimedia (Fruh.)	+		+	+	+	+	+
Junonia c. coenia (Hübner)	+		+	+	+	+	+
Junonia evarete (Stoll)	+	+	+				+
Junonia genoveva (Cramer)		+		+	+	+	+
Anartia jatrophae guantanamo (Munr.)	+	+	+	+	+	+	+
Anartia chrysopelea (Hübner)	+	+					
Siproeta stelenes biplagiata (Fruh.)	+	+	+	+	+	+	+
Phyciodes phaon (Edwards)		+	+				+
Anthanassa frisia (Poey)	+		+	+			+
Euptoieta h. hegesia (Cramer)	+	+	+	+	+		+
Heliconiidae							
Heliconius charitonia ramsdeni (Comstock & Brown)	+	+	+	+	+	+	+
Dryas iulia nudeola (Bates)	+	+	+	+	+	+	+
Agraulis vanillae insularis (Maynard)	+	+	+	+	+	+	+
Libytheidae							
Libytheana motya (Boisd. & Lec.)	++		+	+		+	+
Lycaenidae							
Eumaeus atala (Poey)	+	+				+	
Allosmaitia c. coelebs (H-Schäffer)				+			+
Strymon martialis (H-Schäffer)	+				+		+
Strymon limenia (Hewitson)							+
Strymon columella cybira (Hew.)	+			+	+	+	+
Electrostrymon a. angelia (Hew.)	+	+		+	+		+
Leptotes cassius theonus (Lucas)	+	+		+	+	+	+
Hemiargus hanno filenus (Poey)	+	+	+	+	+	+	+
Nesiostrymon c. celida (Lucas)	++						
Cyclargus a. ammon (Lucas)	+	+	+	+	+	+	+
Brephidium exilis isophthalma (H-S.)			+				

Table 1.—*Continued.*

Taxon	1910–1913	1975–1976		1993–1995			
		Other	South	North	East	West	South
Pieridae							
Ascia monuste eubotea (Godart)	+	+	+	+	+	+	+
Appias drusilla poeyi (Butler)	+	+		+	+	+	+
Eurema nise (Cramer)		+	+	+	+		+
Eurema daira palmira (Poey)	+	+	+	+	+	+	+
Eurema lisa (Boisduval & Leconte)	+	+	+	+	+	+	+
Eurema lucina (Poey)	+			+	+		
Eurema amelia (Poey)	+		+				
Eurema messalina (Fabricius)	+			+	+	+	+
Durema d. dina (Poey)	+	+	+	+	+		+
Eurema boisduvaliana (C. & R. Felder)					+		
Eurema proterpia (Fabricius)					+		+
Eurema nicippe (Cramer)	+	+	+	+	+		+
Nathalis iole (Boisduval)		+	+				+
Kricogonia lyside (Godart)						+	
Anteos maerula (Fabricius)		+	+				
Anteos clorinde (Fruhstorfer)		+			+	+	
Phoebis philea (Linnaeus)					+	+	
Phoebis argante fornax (Butler)	+						
Phoebis agarithe antillia (Brown)		+	+	+	+		+
Phoebis s. sennae (Linnaeus)	+	+	+	+	+	+	+
Aphrissa o. orbis (Poey)	+	+					+
Aphrissa neleis (Boisduval)	+			+	+		+
Aphrissa statira cubana (D'Almeida)	+			+	+		+
Papilionidae							
Battus polydamas cubensis (Dufrane)		+	+	+	+		+
Battus devilliers (Godart)		+	+		+		
Heraclides aristodemus temenes (God.)		+					
Heraclides androgeus epidaurus (G. & S.)		+	+				+
Heraclides a. andraemon (Hübner)	+	+	+	+	+	+	+
Heraclides caignuanabus (Poey)		+	+	+	+		+
Protesilaus celadon (Lucas)	+	+					+
Hesperiidae							
Phocides pigmalion batabano (Luc.)	+		+				+
Proteides mercurius sanantonio (Luc.)	+			+	+		+
Proteides maysi (Lucas)	+			+	+		+
Polygonus leo savigny (Latreille)	+			+	+		+
Urbanus proteus domingo (Scudder)	+	+	+	+	+	+	+
Urbanus dorantes santiago (Lucas)	+	+	+	+	+	+	+
Aguna asander haitensis (Mab. & Boul.)	+	+	+		+		+
Aguna claxon (Evans)							+
Astraptes anaphus anausis (G. & S.)		+	+	+	+		
Astraptes cassander (Fabricius)	+	+					
Astraptes h. habana (Lucas)	+	+		+			+
Astraptes talus (Cramer)					+		
Burca c. concolor (H-Schäffer)						+	
Gesta g. gesta (Evans)					+		
Achlyodes mithridates papinianus (Poey)				+	+		+
Ephyriades arcas philemon (Fabr.)	+						
Ephyriades b. brunnea (H-Schäffer)	+			+	+		+
Pyrgus o. oileus (Linnaeus)	+	+	+	+	+	+	+
Pyrrhocalles antiqua orientis (Skin.)	+	+	+	+	+		+
Perichares philetes (Gmelin)				+			+

Table 1.—*Continued.*

Taxon	1910–1913	1975–1976		1993–1995			
		Other	South	North	East	West	South
Synapte m. malitiosa (H-Schäffer)				+			+
Cymaenes tripunctus (H-Schäffer)	+			+	+	+	+
Oarisma nanus (Herrich-Schäffer)	+	+					
Hylephila phyleus (Drury)	+	+	+	+			+
Polites b. baracoa (Lucas)	+			+			+
Atalopedes m. mesogramma (Latr.)	+			+			+
Wallengrenia misera (Lucas)	+			+	+		+
Parachoranthus magdalia (H-S.)							+
Choranthus radians (Lucas)		+	+	+	+	+	+
Euhpyes c. cornelius (Latreille)	+		+	+	+	+	+
Asbolis capucinus (Lucas)	+		+		+		+
Panoquina sylvicola (H-Schäffer)	+			+	+		+
Panoquina corrupta (H-Schäffer)	+			+	+		
Panoquina o. ocola (Edwards)	+						
Panoquina p. panoquinoides (Skinner)							+
Nyctelius n. nyctelius (Latr.)				+			+
Lerodea eufala (Edwards)	+	+		+			+

ical groups (north, east, west), and more detailed descriptions of these, and of localities south of the Ciénaga, are given below. Locality names and roads and tracks used in 1993–1995 are shown in Figure 1.

Northern Group

The principal northern locality was the forested region at El Abra (Fig. 2) near Nueva Gerona, at the southernmost end of the Sierra de Casas, together with adjoining tracks and fields. While it is probable that little primary forest remains even on the steeper slopes, areas of mature secondary forest are present. Other parts of this Sierra are largely deforested and marble quarrying is impacting the hills (Fig. 4). The El Abra locality has been notably species-rich on each visit, and accounts for most species recorded from the north. The forest on the nearby Sierra de Caballos is heavily damaged and was unproductive. A fringe of secondary woodland and open scrub on the northeast coast at Playa Bibijagua was moderately diverse, but contributed no species not found more frequently at El Abra. West of Nueva Gerona along the north coast, the land is almost entirely farmed or cultivated, and was extremely depauperate in butterflies.

Eastern Group

A second species-rich area of newer and more open secondary forest and scrub lies southeast of La Reforma (Fig. 5); to the east, patches of well-preserved forest merge with a coastal mangrove belt. This area, and cleared hillside west of the town, and areas south to the edge of the Ciénaga de Lanier have contributed most records from the east of the island. Sampling also was carried out in uniformly species-poor agricultural land and citrus plantations, at intervals along the road from La Fé to Cayo Piedra.

Western Group

Sampling was performed along road margins from Nueva Gerona to Playa Rojas (Colony), passing through the Sierra de La Cañada, near La Demajagua,

Fig. 2–5.—2. Edge of recent secondary forest at El Abra, with forested hill of the Sierra de Casas. 3. Low vegetation and exposed limestone in the Ciénaga de Lanier near Cayo Piedra, late in the dry season (March). Such areas are extensively flooded during the wet season. 4. Marble quarrying and agriculture in the Sierra de Casas, near El Abra. Note residual forest on hill slopes to the left. 5. Open secondary forest near La Reforma.

and from La Fé to the nature preserve of Los Monos, at the edge of the Ciénaga and marking the northern fringe of the forest covering the south of the island. A protected white-sand area near Río los Indios, including original pinewoods, still supports *Eumaeus atala,* but *Oarisma nanus* was last seen there in 1976. Western areas are generally heavily cultivated and species-poor, including the plantations of pine that now largely replace the original stands of the Sierra de La Cañada and elsewhere. The species list compiled for the western region was the most limited; no areas approaching the diversity of El Abra and La Reforma were found.

Southern Group

Localities visited in the low, densely forested southern part of the island generally followed the few established roads and tracks (Fig. 1). Although in places the forest is secondary growth produced by felling for charcoal burning, near present or former small settlements, much of this forest is undisturbed. Localities surveyed within the forest include: from Cayo Piedra to the meteorological station at Punta del Este and Cerro Caudal, Rincón de Guanal, Carapachibey, from Cocodrílo to Hato Milián (Fig. 6), and Pedernales (Fig. 7), approaching the tip of the southwestern peninsula. Mangrove and coastal scrub were sampled near Punta del Este, and cleared areas, on the track towards Playa Blanca, at Rincón de Guanal, Hato Milián, and Lugo (near Punta de Pedernales). The distribution of species across the southern zone was not uniform: the forest in the extreme east, around Punta del Este, was unaccountably poor during our visits (other than the slightly elevated area of Cerro Caudal), and species richness increased towards the west, with greatest diversity from Carapachibey to Hato Milián and Punta de Pedernales.

We did not attempt to survey the Ciénaga de Lanier, which in the wet season is extensively flooded and includes expanses of sawgrass and in the dry season (Fig. 3) contains wide areas of exposed limestone supporting few flowers as nectar sources. Brief excursions into the swamp yielded few butterflies, and all of species found more plentifully elsewhere.

RESULTS AND DISCUSSION

The Species List in Holland (1916)

Before discussing the results of recent surveys (Table 1), several points arising from the account by Holland (1916) need brief commentary. These concern changes in nomenclature and corrections resulting from our examination of Holland's material in Carnegie Museum. It should be borne in mind that at the time of Holland's work distributional information on Antillean butterflies was often incomplete, and taxonomic arrangement of some groups has been revised subsequently.

A few taxa cited by Holland were misidentified: *Lucinia sida* was listed as *L. cadma,* a Jamaican endemic; and his "*Anartia lytrea*" is actually the Cuban endemic *A. chrysopelea.* Holland's specimens of *Junonia coenia genoveva* proved to be *J. evarete* (sensu Turner and Parnell, 1985). The hairstreak specimen listed by Holland as "*Thecla favonius*" is instead the Cuban subspecies of *Electrostrymon angelia.* Holland regarded Link's series of the common pierid *Eurema daira palmira* as *E. elathea,* a similar species occurring in the far east of Cuba. Another *Eurema* that requires comment is Holland's "albino female" of "*Terias citrina*";

Fig. 6, 7.—6. Edge of the semideciduous limestone forest on the southwestern peninsula, from the cleared Guardia Forestal settlement at Hato Milián. 7. Low, exposed coastal limestone reef on the southwestern peninsula, near Punta de Pedernales. The coastal scrub vegetation merges with the semideciduous forest, often via a mangrove belt (Fig. 1).

we reidentified this specimen as *E. messalina,* a species now widespread on the Isle of Pines. Early records of another pierid group, the genus *Phoebis,* also call for clarification. The four specimens in Link's collection listed by Holland as "*Catopsilia agarithe fornax*" are correctly of the Cuban endemic *Phoebis argante fornax.* The collection studied by Holland does not include *P. agarithe antillia,* now widespread on the Isle of Pines, while *P. argante* has not been found there subsequently. Holland's "*Catopsilia editha*" instead represents *Aphrissa neleis,* now locally common on the Isle of Pines, and his "*Catopsilia neleis*" actually pertains to *Aphrissa statira,* a species more common than *A. neleis.* Two hesperiids described by Holland as new, supposedly endemic taxa require commentary: "*Telegonus geronae*" and "*Amblyscirtes insulae-pinorum*" were later recognized

(Alayo and Hernández, 1987) as synonyms, respectively, of *Astraptes cassander* and *Euphytes c. cornelius,* also present on the main island. Lastly, *Eurema priddyi* was decribed from Haiti (Lathy, 1898) and a subspecies *forbesi* was described later from Isle of Pines specimens (Klots, 1929). We regard *E. priddyi forbesi* as a synonym of *E. lucina*; the latter was included in Holland's list and still occurs on the island.

The Fauna and Seasonality

In all, 111 butterfly species have been recorded to date on the Isle of Pines, of which we have seen 106 in the field (Table 1). In summary, to Holland's list of 65 species may be added early specimens of *Libytheana motya, Eunica monima,* and *Nesiostrymon celida* that we have found in museum collections, bringing the total for species recorded in the first two decades of the century to 68 (Table 1). Fieldwork in 1975–1976, which included the southern forest for the first time, added 25 species to the island's list, and 18 more have been added from 1993 to 1995.

Two of our recent visits took place in the wet season (in July and August) and two others occurred late in the dry season (March). As in other Antillean islands, regular recording is essential to provide a picture of the seasonality or phenology of Isle of Pines butterflies. Nonetheless, the expected overall reduction in numbers of adult butterflies (individuals on the wing) in the dry season is marked. Much of our summer visit in 1993 was spent in a broad survey that included species-poor northern localities and yielded only 54 species records. A more representative tally of 87 species was recorded in summer 1995, while the dry season visits yielded 62 and 55 species, respectively.

Conditions in all localities visited in March 1995 were extremely parched after prolonged drought; numbers of butterflies were generally low. However, on the southwestern peninsula the most frequent skipper was *Proteides maysi,* generally considered rare, but outnumbering "common" species such as *Pyrgus oileus* and *Urbanus dorantes.* Such transient anomalies exemplify the unbalanced view of a fauna that can result from a brief period of fieldwork. At this time, however, flowers of *Eupatorium odoratum, Bidens alba, Stachytarpheta jamaicensis,* and species of *Solanum* were newly opening, and while most specimens of some species (e.g., *Marpesia eleuchea, Anartia jatrophae, Siproeta stelenes, Dryas iulia, Strymon columella, Heraclides andraemon, Polygonus leo, Urbanus dorantes, U. proteus,* and *Wallengrenia misera*) were very worn, others (e.g., *Doxocopa laure, Heliconius charitonia, Appias drusilla, Phoebis sennae, Protesilaus celadon, Proteides mercurius, P. maysi, Achlyodes mithridates,* and *Ephyriades brunnea*) were uniformly fresh, suggesting that the onset of emergence of some species is synchronized with availability of plentiful nectar prior to the spring rains.

Most species were recorded in varying numbers during both wet and dry seasons. Most are evidently at least bivoltine, some continuously brooded. Some taxa were recorded on only one visit; e.g., *Anetia briarea* and *Aguna claxon* were seen only in March 1994, and *Astraptes talus* was locally abundant in the east in August 1994 but absent from the same locality in March 1995. Analysis of voltinism must await data on localities worked at regular intervals. Moreover, marked fluctuations in timing of emergence from year to year is well known in Antillean butterfly faunas (Schwartz, 1989; Smith et al. 1994*b*). Where voltinism is well documented on the main island, as for *E. celadon,* the spring emergence is

matched on the Isle of Pines; an infrequent, second emergence documented on the main island has yet to be recorded on the Isle of Pines.

Regional Distribution

Despite the incompleteness of data on voltinism, cumulative records from the past 20 years provide a picture of the regional distribution of the 106 recorded species. In all, 91 species have been found south of the Ciénaga de Lanier, and 96 from pooled localities north of this ecological divide. During 1993–1995, 81 species were recorded from northern and eastern localities combined whereas only 32 species were documented for western localities. The richness of the south is indicated by the fact that this zone represents only 33% of the island's area and that it received only one-third of our field time during recent visits. Furthermore, sampling is more difficult in the southern terrain, compounding the likelihood of overlooking very local species or missing species not in flight during our visits.

The richness of the little-disturbed southern area is not surprising; more remarkable was the discovery that the region north of the Ciénaga supports a butterfly fauna comparable with that of the southern forest. Although the land area of the north is almost twice that of the south, its long history of habitation, farming and cultivation, recent extensive conifer planting, citrus sylviculture, and inundation by damming of rivers might be expected to have reduced species diversity. However, we suggest that this northern diversity is extremely precarious and markedly concentrated in a few very small areas: El Abra south of Nueva Gerona, near La Reforma in the east; and to a lesser degree in pockets of secondary woodland at Playa Bibijagua. Each of these sites is very vulnerable to land clearance; less than one mile from the El Abra locality, a component hill of the Sierra de Casas has been half-removed by marble quarrying (Fig. 4), and another entirely leveled since 1976. Elsewhere, we have seen encroachment into these unprotected areas between July 1993 and March 1995, and were they to be destroyed, we believe that species diversity at present collectively credited to the north of the island would decline precipitously to the low level now seen in the highly disturbed localities characterizing much of the island above the Ciénaga de Lanier.

It seems likely that these isolated, species-rich enclaves support relict faunas, surviving from the time when the northern hill ranges were covered in primary deciduous and pine forests, presumably including other varied ecosystems in the northern lowlands. If so, it is remarkable that such relatively small areas, now by no means undisturbed, should have preserved their present level of diversity. It is possible that the fauna of the southern zone has acted as a reservoir in maintaining this level, since the narrow Ciénaga de Lanier is unlikely to offer any barrier to movement of most butterflies in either direction.

The numbers of species recorded north and south of the Ciénaga are similar, but to what extent is the fauna of the island homogeneous? At present, 18 species are known from the north but not the south, and seven conversely. In the former group, *Eumaeus atala* and *Oarisma nanus* occur only in lateritic pineland, not present in the south, and *Burca braco* may be restricted to open, dry western sandy areas. *Anetia briarea, Calisto sibylla, Marpesia chiron,* and *Heraclides aristodemus* are generally upland species in Cuba, while *Historis acheronta* is more frequent in forest more moist than that of the south. *Anartia chrysopelea,* a butterfly of the forest edge, was common and widespread in 1975–1976 but has not been seen on the island subsequently. The southern zone does not include the

open land in which *Battus devilliers* is most frequent on the main island, or the disturbed land most suited to *Eurema lucina.* Southern localities apparently suitable for *Hamadryas amphicloe, Lucinia sida, Eurema boisduvaliana, Astraptes cassander, A. talus, Gesta gesta,* and *Panoquina corrupta* are present, and most of these species, so far unrecorded from the south, may prove to occur there.

Of the species known only south of the Ciénaga, ecological ties are even less obvious. *Danaus eresimus* was found only in the southern edge of the Ciénaga, but probably occurs along both margins of this swamp. *Eurema amelia* was collected by Link at Nueva Gerona and Los Indios and recorded from the southern forest in 1975–1976, but since then has not been seen on the island. *Brephidium exilis* is restricted to salt marshes and may also occur in the north; a similar situation pertains to the mainly coastal *Panoquina panoquinoides. Kricogonia lyside,* a strong dispersalist, is unlikely to be limited to the southern forest when populations are large. Both *Strymon limenia* and *Parachoranthus magdalia* are ecologically tolerant; each has been found only once in the south and may well have been overlooked in the north. The Central American *Aguna claxon,* however, probably a recent colonist, also has become established in the dry forest of the Guanahacabibes Peninsula (Hernández et al., 1994), ecologically similar to that of the south of the Isle of Pines.

Faunal Size and Comparisons

In considering the butterflies recorded from the Isle of Pines, while a single species number provides an index to overall diversity, its significance needs to be qualified. While the size of an island fauna may reflect a balance between colonization and extinction (Munroe, 1948, 1953; MacArthur and Wilson, 1963, 1967), these processes are seldom recognizable as discrete events within incompletely documented faunas (Smith et al., 1994*a*), particularly where phenology is little known. As for any Antillean butterfly faunal list, the present species total of 111 for the Isle of Pines is provisional, likely to increase with future work. In August 1994, six species were newly recorded from the island: *Historis acheronta, Eurema proterpia, Aguna claxon, Astraptes talus, Gesta gesta,* and *Parachoranthus magdalia.* While *Phoebis argante, Ephyriades arcas,* and *Lerodea eufala* have not been seen since the Carnegie expeditions, and the early record of *Nesiostrymon celida* has yet to be repeated, it cannot be assumed that any of these taxa is now extinct. For example, *Strymon martialis* was found in August 1994, the first record since May 1912.

The present species list for the Isle of Pines, albeit provisional, provides a basis for comparing biodiversity with other subsets of the Cuban fauna and for consideration of the origins of the fauna. From the ecological standpoint, the island's fauna may be compared with that of the Guanahacabibes Peninsula, which recently has been studied intensively and tabulated (Hernández et al., 1994). In all, 123 species have been recorded from the two areas combined, of which 86 (70%) are common to both. Sixteen species are known from Guanahacabibes but not from the Isle of Pines, while 21 are recorded on the Isle of Pines but not on the mainland peninsula. The area of Guanahacabibes Park (780 km^2) is almost identical to that of the southern forest of the Isle of Pines (ca. 0.7% of the total land area of Cuba), and each includes well-preserved, semideciduous limestone forest with coastal limits (Samek, 1973) and is located adjacent to long-cultivated land. Both areas have suffered minimal human alterations and currently share some

degree of protection. Their faunas, however, while approximately similar in size, are distinctive. The Guanahacabibes forest has been surveyed more intensively, and at present 101 butterfly species have been recorded there. Some 19 species are known from Guanahacabibes that have not been recorded from the southern forest of the Isle of Pines, and the same number conversely. Each of the two regions supports about 40 Cuban specific or subspecific endemics, or over half the total for Cuba. Among the major families, the proportional representation of danaids, nymphalids, and papilionids of Cuba as a whole is almost identical in the two regions. The higher species count for the Isle of Pines largely reflects diversity of lycaenids and hesperiids; the insular fauna includes 70% of the Cuban total for each family, a somewhat better representation than at present known from Guanahacabibes.

A noteworthy aspect of the butterfly fauna of the Isle of Pines is its lack of obvious evolutionary divergence from that of the main island. Throughout the West Indies, inter-island gaps narrower than the Gulf of Batabanó frequently have provided sufficient isolation for divergence (Smith et al., 1994*a,* 1994*b*). Two hesperiids described by Holland (1916) as new were later synonymized with two other taxa (Table 1). Alayo and Hernández (1987) suggested that another skipper, *Pyrrhocalles antiqua,* may differ subspecifically on the Isle of Pines from the main island subspecies *orientis,* but enlarged series now available show no divergence. Indeed, examination of series of all butterfly taxa from the Isle of Pines and Cuba as a whole demonstrates the phenotypic homogeneity of these often widely separated populations. We believe that the reason for this lies in the geologic history of the Isle of Pines and its pattern of colonization.

Origins of the Fauna

We suggest that the lack of divergence of Isle of Pines butterfly populations from those in Cuba stems from the hydrographic profile and history of the Gulf of Batabanó. The unnavigability of this stretch of water was recognized by mariners, and on early maps the Isle of Pines was sometimes represented as a peninsula of the south coast of Cuba (Jiménez, 1976). At its deepest, the gulf is only 10 m, and much is as shallow as 2–3 m (Anonymous, 1991). Lowering of sea water would have provided substantial land links with Cuba many times during the Pleistocene glaciation cycles, while the ancient high land of the Sierras, at least, would have remained emergent and accessible to dispersal from the main island during interglacial periods. During the last full glacial period (ca. 20,000 YBP), when the Florida peninsula was twice its present area (Webb, 1990), the Isle of Pines and Cuba would have been substantially linked (Webb, personal communication), and overland exchange of biotas would have been possible, whether or not the hills acted as refugia for earlier colonists. Also, air-borne dispersal presumably continues to contribute to colonization, but the means of colonization used by each taxon in the present fauna remains unknown. However, it may be inferred that the two *Calisto* of the Isle of Pines, members of a sedentary genus showing no ability to disperse over water throughout its range (Smith et al, 1994*a*), arrived overland. Whatever routes were followed in establishing the present butterfly fauna, the history of colonization seems to have been insufficiently long, or isolation sufficiently effective, for obvious evolutionary divergence to have made an imprint on the island's butterflies.

Genetic Comparisons

Wing pattern is the character most widely used in descriptions of island butterfly subspecies. However, morphological or phenotypic similarity may mask divergence at the genetic level. Davies (1995) analyzed populations of *Anartia jatrophae, Dryas iulia,* and *Heliconius charitonia* on the Isle of Pines and on the main island of Cuba using enzyme electrophoresis. Each of these species has evolved island races in the West Indies, most notably *Dryas iulia* with 12 named subspecies across the islands (Smith et al., 1994*a*). The results of the survey indicate, however, that extremely little genetic differentiation for populations of sampled taxa between Cuba and the Isle of Pines. This is consistent with earlier phenotypic assessment which grouped Isle of Pines populations with the Cuban races: *A. j. guantanamo, D. i. nudeola,* and *H. c. ramsdeni.* Despite the overall genetic similarity for each of these three species, samples from the Isle of Pines were more similar to samples from nearby western Cuba than to those from eastern Cuba. This suggests that, for these butterflies at least, a short water barrier has been a less significant factor in permitting genetic change than overall distance. The observed close genetic similarity may reflect significant gene flow between western Cuba and the Isle of Pines through dispersal, relatively recent colonization, and/or minimal genetic divergence between originally contiguous populations that became separated after the loss of the last Pleistocene land link.

In introducing the Isle of Pines butterflies collected for Carnegie Museum, Holland (1916) noted that they ". . .seem scarcely to adequately represent what must be a rather rich fauna, if we are justified in drawing conclusions from what we know of the wealth of insect-life which is found in Cuba," and surmised that his list might lay the foundation for a more complete account in the future. We conclude that his forecast was correct, with two-thirds of the total list of Cuba's butterfly species and with a good representation of endemic taxa now recorded from this small island. We, in turn, forecast that phenological and genetic studies will prove critical to the enhancement of our understanding of the island's butterflies. Moreover, continued monitoring is needed to document the future of extremely localized and equally vulnerable taxa in the north. Whether or not the latter survive, conservation of the remarkably preserved southern forest will maintain much of the richness of the butterfly fauna of the Isle of Pines.

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LITERATURE CITED

ALAYO, P. D., AND L. R. HERNÁNDEZ. 1987. Atlas de las mariposas diurnas de Cuba (Lepidoptera: Rhopalocera). Editorial Científico-Técnica, Ciudad de La Habana, Cuba.

ANONYMOUS. 1991. Folio No. 2597: Cuba. Admiralty Charts and Publications, London, United Kingdom.

BRITTON, N. L. 1916. The natural vegetation of the Isle of Pines, Cuba. Journal of the New York Botanical Garden, 18:64–71.

BRUNER, L. 1919. Saltatorial Orthoptera from South America and the Isle of Pines. Annals of Carnegie Museum, 13:5–91.

DAVIES, N. 1995. Origins of Diversity: The Evolutionary Genetics of Caribbean Butterflies. Unpublished Ph.D. Dissert., University College, London, United Kingdom.

GILTNER, L. C. 1904. Map showing relative distances from the Isle of Pines to the United States, Mexico, Central America and the West Indies. Matthews-Northrup, Buffalo, New York.

GORT, S. A., T. ESCOBAR, J. IZQUIERDO, M. CORREOSO, AND N. SINGH. 1994. Isla de la Juventud. Su naturaleza. Editorial Científico-Técnica, Ciudad de La Habana, Cuba.

HEIDEMANN, O., AND H. OSBORN. 1917. Rhynchota of the Isle of Pines. Annals of Carnegie Museum, 11:346–355.

HERNÁNDEZ, L. R., D. S. SMITH, N. DAVIES, AND A. ARECES-MALLEA. 1994. The butterflies and vegetational zones of Guanahacabibes National Park, Cuba. Bulletin of the Allyn Museum, 139: 1–19.

HOLLAND, W. J. 1916. The Lepidoptera of the Isle of Pines, being a list of the species collected on the island by Mr. J. L. Graf and Mr. G. A. Link, Sr. in 1910 and 1912–3. Annals of Carnegie Museum, 10:487–518.

HOLLAND, W. H., AND H. KAHL. 1916. A list of the Orthoptera collected in the Isle of Pines by J. L. Graf, 1910, and G. A. Link, 1912–1913. Annals of Carnegie Museum, 10:541.

HOLLAND, W. J., AND E. A. SCHWARZ. 1917. List of the Coleoptera collected on the Isle of Pines by Gustav A. Link Sr., 1912–1913. Annals of Carnegie Museum, 11:333–345.

JENNINGS, O. E. 1917. A contribution to the botany of the Isle of Pines, Cuba, based on the specimens of plants from that island contained in the herbarium of the Carnegie Museum under date of October, 1916. Annals of Carnegie Museum, 11:19–290.

JIMÉNEZ, A. N. 1976. Isla de Pinos: Pirates, Colonizadores, Rebeldes. Editorial Arte y Literatura, La Habana, Cuba.

KAHL, H. 1916. A list of the Odonata collected on the Isle of Pines by Mr. J. L. Graf in 1910, and by Mr. G. A. Link in 1912–1913, now contained in the Carnegie Museum. Annals of Carnegie Museum, 10:519–526.

KLOTS, A. B. 1929. A revision of the genus *Eurema* Hübner. Entomological Americana (New Series), 9:99–163.

LATHY, P. I. 1898. A new species of *Terias* from Haiti. The Entomologist's Monthly Magazine (Second Series), 9:223.

LEWIS, J. F., AND G. DRAPER. 1990. Geology and tectonic evolution of the northern Caribbean margin. Pp. 77–140, *in* The Geology of North America, Volume H: The Caribbean Region (G. Dengo and J. E. Case, eds.). The Geological Society of America, Boulder, Colorado.

MACARTHUR, R. H., AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. Evolution, 17:373–387.

———. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

MUNROE, E. G. 1948. The Geographical Distribution of Butterflies in the West Indies. Unpublished Ph.D. Dissert., Cornell University, Ithaca, New York.

———. 1953. The size of island faunas. Pp. 52–53, *in* Proceedings of the Seventh Pacific Science Congress of the Pacific Science Association, Volume IV. Zoology. Whitcome and Tombs, Auckland, New Zealand.

PICHARDO, D. E. 1860–1872. Isla de Cuba. Carta Geotopográfica. (Facsimile 1970). Habana, Cuba.

POEY, P. 1854*a*. Apuntes sobre la fauna de la Isla de Pinos. Memorias Historia Natural de la Isla de Cuba, 1:424–431.

———. 1854*b*. Apuntes sobre la fauna de la Isla de Pinos (Apéndice). Memorias Historia Natural de la Isla de Cuba, 1:433–453.

———. 1861. Apuntes sobre la fauna de la Isla de Pinos (Art. LIII, Apéndice). Memorias Historia Natural de la Isla de Cuba, 2:415–427.

ROHWER, S. A., AND W. J. HOLLAND. 1917. List of the Hymenoptera collected on the Isle of Pines by

G. A. Link, Sr., 1912–1913, and contained in the Carnegie Museum. Annals of Carnegie Museum, 11:291–296.

SAMEK, V. 1973. Regiones fitogeográficas de Cuba. Serie Forestal Numéro 15, Academia de Ciencias de Cuba, Departamento de Ecologia Forestal, Habana, Cuba.

SCHWARTZ, A. 1989. The Butterflies of Hispaniola. University of Florida Press, Gainesville, Florida.

SMITH, D. S., L. D. MILLER, AND J. Y. MILLER. 1994*a*. The Butterflies of the West Indies and South Florida. Oxford University Press, Oxford, United Kingdom.

SMITH, D. S., S. J. RAMOS, AND F. MCKENZIE. 1994*b*. The butterflies of Mona Island (Puerto Rico) and an approach to their origins and phenology. Caribbean Journal of Science, 30:95–103.

TURNER, T. W., AND J. R. PARNELL. 1985. The identification of two species of *Junonia* Hübner (Lepidoptera: Nymphalidae): *J. evarete* and *J. genoveva* in Jamaica. Journal of Research on the Lepidoptera, 24:142–153.

WEBB, S. D. 1990. Historical biogeography. Pp. 70–100, *in* Ecosystems of Florida (R. L. Myers and J. J. Ewell, eds.). University of Central Florida Press, Orlando, Florida.